

## Jaws and Teeth of *Australopithecus afarensis* From Maka, Middle Awash, Ethiopia

TIM D. WHITE,<sup>1\*</sup> GEN SUWA,<sup>2</sup> SCOTT SIMPSON,<sup>3</sup>  
AND BERHANE ASFAW<sup>4</sup>

<sup>1</sup>Laboratory for Human Evolutionary Studies, Museum of Vertebrate Zoology, and Department of Integrative Biology, University of California, Berkeley, California 94720-3140

<sup>2</sup>University Museum, University of Tokyo, Hongo, Bunkyo-ku, Tokyo 113, Japan

<sup>3</sup>Department of Anatomy, Case Western Reserve University, Cleveland, Ohio 44106-4930

<sup>4</sup>Rift Valley Research Service, Addis Ababa, Ethiopia

**KEY WORDS** mandible; Pliocene; hominid; dentition; Afar

**ABSTRACT** The Maka locality in Ethiopia's Middle Awash area has yielded new craniodental remains dated to 3.4 million years (myr) in age. These remains are described and assessed functionally and systematically. The fossils are assigned to *Australopithecus afarensis*. Maka thus joins Hadar and Laetoli as the third major locality yielding this species. As with previous site samples, the Maka collection displays a wide range of size variation. The nearly complete and undistorted MAK-VP-1/12 adult mandible from Maka is an excellent match for Hadar and Laetoli counterparts, confirming the geographic and temporal distribution of *A. afarensis*. This specimen shows that this taxon is functionally and developmentally hominid in its incisor/canine/premolar complex. A postulated evolutionary trajectory through *A. anamensis* to *A. afarensis* would have involved postcanine megadontia and other adaptations to a more heavily masticated diet relative to the earlier *Ardipithecus ramidus*. *Am J Phys Anthropol* 111:45–68, 2000. © 2000 Wiley-Liss, Inc.

When the species *Australopithecus afarensis* was named in the late 1970s, mandibles and teeth played a key role in its diagnosis and description (Johanson and White, 1979; Johanson et al., 1978, 1982a). The ensuing decade witnessed debates over the unity and phylogenetic relationships of this taxon (summarized by Boaz, 1988). The geographic separation of Laetoli and Hadar, and the variation seen in the *A. afarensis* paratype series, led some investigators to suggest that multiple species had been pooled (see discussion in White, 1985). The reopening of paleoanthropological research in Ethiopia in 1990 allowed continuation of research in the Maka catchment of the Middle Awash paleoanthropological study area of Ethiopia.

Pliocene hominids were discovered at Be-lahdelie and Maka on the eastern side of the

Middle Awash paleoanthropological study area in 1981 (Asfaw, 1987, 1988; Clark et al., 1984; White, 1984). A return to Maka in the autumn of 1990 resulted in the recovery of additional remains, including teeth and jaws attributed to *A. afarensis*. These specimens have been precisely placed in a refined chronostratigraphic sequence (White et al., 1993; Renne et al., 1999). Subsequent research on the western side of the study area, at Ara-

Grant sponsor: National Science Foundation; Grant sponsor: Japanese Society for the Promotion of Science; Grant sponsor: Japanese Ministry of Education, Science, Sports, and Culture; Grant sponsor: CWRU Research Initiation Grant Program; Grant sponsor: University of California Collaborative Research Program of the Institute of Geophysics and Planetary Physics at Los Alamos National Laboratory.

\*Correspondence to: Tim White, Department of Integrative Biology, 3060 VLSB, University of California at Berkeley, Berkeley, CA 94720-3140. E-mail: timwhite@socrates.berkeley.edu

Received 23 June 1998; accepted 19 August 1999.



Fig. 1. A view toward the north of the Maka sands in the upper Maka catchment. Arrow indicates a paleontologist in a white hat at the discovery site of the MAK-VP-1/12 mandible. A lens of the Sidiha Koma Tuff (SHT), dated to 3.4 myr, is interfingered in these sands and constrains the age of the Maka hominids.

mis, Sagantole, and Kuseralee Dora, has yielded remains of hominids attributed to *Ardipithecus ramidus* (White et al., 1994, 1995; WoldeGabriel et al., 1994, 1995). Maka provides the first substantial sample of *A. afarensis* remains outside of the paratype sites of Hadar and Laetoli. The Maka fossils provide fresh data bearing on systematic and functional issues surrounding *A. afarensis*.

The Maka described here sample a time period, (3.0–3.6 million years ago) (myr), that has now yielded fairly abundant fossils that have already been afforded detailed description in this journal. We subscribe to interpretations that recognize *A. afarensis* as the only documented species of early hominid occupying that time period. The mandibles and teeth of *A. afarensis* are well-known, and specimens recovered in the 1970s are fully described elsewhere (White, 1977, 1980, White and Johanson, 1982; Johanson et al., 1982b; Suwa, 1990; Suwa et al., 1994, 1996). As will be seen in the comparative descriptions to follow, the Maka

remains depart in no anatomically significant way from *A. afarensis* as defined by the Hadar and Laetoli hypodigm. However, they do offer significant new insights into functional and systematic issues surrounding that taxon.

### PROVENIENCE

The Maka specimens described here were surface finds, but preservational characteristics and their relationship to the eroding sediments clearly indicate that they were embedded in the sands and gravels referred to informally as the "Maka sands" of the Matabaietu Formation. These faunally-rich sand and gravel deposits represent pedialluvial aggradation into an area of the Middle Awash previously occupied by extensive, relatively deep lakes. The Maka sands were deposited disconformably about 7 m above the Cindery Tuff, and 6 m above the VT-3 (= Wargolo) tuff horizons (Fig. 1). These tuffs are dated to  $3.85 \pm 0.083$  and  $3.74 \pm 0.023$  myr, respectively (White et al., 1993). Interdigitated with the hominid-bearing

Maka sand unit is a volcanic lens, MA90-16, whose glass chemistry we correlate with the Sidiha Koma Tuff near the base of the Hadar Formation, and with tuff MA90-28 at the nearby Wee-ee fossil locality (White et al., 1993). These units are dated to  $3.40 \pm 0.03$  myr and  $3.39 \pm 0.036$  myr, respectively (Walter and Aronson, 1993; White et al., 1993). Thus, we have high confidence that the age of the Maka hominids described here is ca. 3.4 myr, just slightly older than the earliest hominids recovered from the base of the Hadar Formation to the north.

### MATERIALS AND METHODS

The 1960s *Homo habilis* controversy appears to have made a lasting impression on many workers who subsequently found and described fossils in eastern Africa. Perhaps reluctant to revisit the heated controversies of the previous decade, 1970s workers published descriptions of hominid fossils that avoided phylogenetic and taxonomic conclusions. A series of publications largely devoid of explicit comparisons or other systematic considerations resulted (e.g., Leakey et al., 1971; Leakey and Wood, 1973; Leakey and Walker, 1973; Day and Leakey, 1973; Day et al., 1976; White, 1977; Johanson et al., 1982a; Leakey and Walker, 1985). Between the initial announcements of fossils (usually in *Nature*) and monographic treatment, the *American Journal of Physical Anthropology* was used as the outlet for the dissemination of information about the new hominids from Koobi Fora, Laetoli, and Hadar. These descriptions apparently were not written to be read as text, but rather to provide detailed published archival inventories of preservational and anatomical characteristics for each specimen.

The avoidance of explicit anatomical comparisons has led to a plethora of specimen descriptions, many of which, in our view, are not helpful. For example, when a retromolar fossa was described as "wide" in a description, did it mean "wide" relative to humans, to gorillas, or to other conspecific individuals? We recognize that, our views notwithstanding, the place and nature of detailed anatomical descriptions in paleoanthropology will continue to be debated and modified as scanning, archiving, and casting technologies advance. Nevertheless, we wish to go on

record as favoring an explicitly comparative approach, which we employ here.

The descriptions that follow are explicitly comparative. All observations concerning specimens discussed below were made on the original fossils. The comparative sample of *A. afarensis* used in this analysis includes all published specimens from Laetoli as well as all Hadar specimens recovered prior to 1990. The original Maka remains are permanently housed in the Paleoanthropology Laboratory at the National Museum of Ethiopia in Addis Ababa. Comparative observations and data on modern ape dentognathic remains were made on the original specimens at the Cleveland Museum of Natural History and additional collections described below.

### PRESERVATION

**MAK-VP-1/2 (Figs. 2, 4b).** Adult right side of a mandible with condyle,  $M_1$ – $M_3$ . The specimen was found in 19 pieces by Yohannes Haile-Selassie on October 10, 1990. The surface is perfectly preserved except for a few root etchings. All joints were good, and there is no residual distortion. The specimen lacks most of the gonial angle and coronoid process, and little of the base remains. The teeth show substantial plant root etching but are otherwise well-preserved and undistorted.

**MAK-VP-1/4 (Fig. 8d).** Right lower  $M_2$ . This specimen was found by Yohannes Haile-Selassie on October 11, 1990. It is a complete crown without roots.

**MAK-VP-1/6 (Fig. 8).** Corpus fragment from the left side of a mandible. The specimen was found by Tim White on October 11, 1990. It is very poorly preserved, with the distal  $M_2$  and total  $M_3$  roots in place, but no tooth crowns. The bone surface is mostly exfoliated.

**MAK-VP-1/12 (Figs. 3–7).** Adult mandible with  $LI_2$ – $M_3$ ,  $RP_3$ – $M_3$ , and both condyles. The specimen was found by Tim White on October 12, 1990. The first segment found was a portion of right corpus with  $M_1$ . After intensive slope collection and sieving, a total of 109 fragments was found to comprise the restored specimen (Fig. 3). With so many sequential glue joints in the ramus, there is

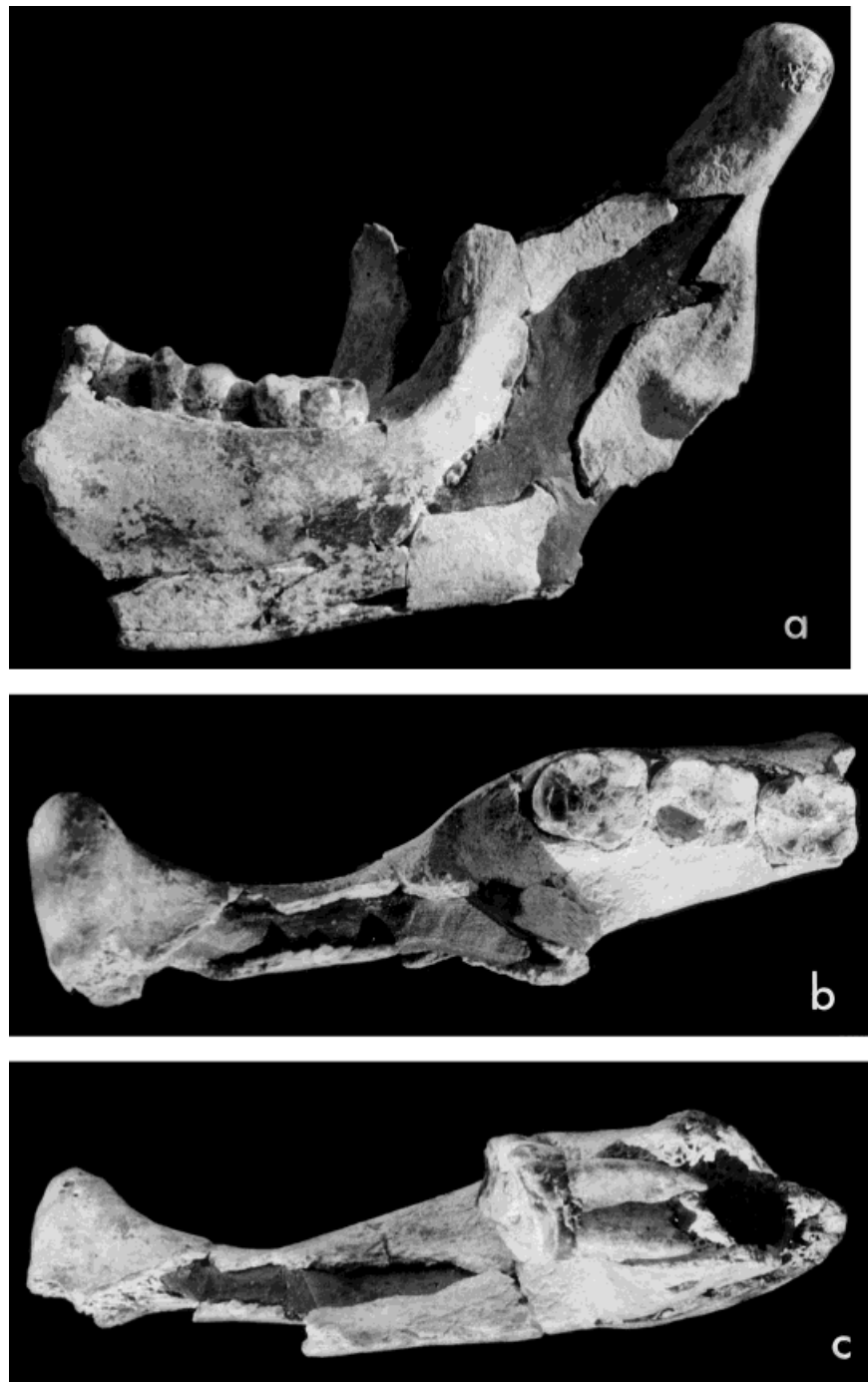


Fig. 2. The MAK-VP-1/2 mandible. **a**: Medial view. **b**: Occlusal view. **c**: Anterior view. All natural size.

probably slight distortion, particularly in the setting of the condyles relative to the dentition. However, the continuity of bony surface indicates that all structures are

within a millimeter of their true position. The coronoid processes and most of both gonial angles are missing. The surfaces of both rami are weathered and crossed by





Fig. 3. Pieces from the MAK-VP-1/12 sieve operation potentially belonging to the hominid mandible. One hundred and nine of these pieces were reassembled to form the mandible.

many fracture lines. The corpus is well-preserved, with some loss of labial alveolar bone across the incisor arcade. Even the thin mental spine is perfectly preserved, but based on previous experience we predict that this fragile structure will be broken by finger or caliper within 3 years of this publication. There is light etching on the bone surfaces, most pronounced on the left corpus, and particularly intensive on the right condyle. The teeth are macroscopically well-preserved. Microscopically they all exhibit various degrees of postdepositional modifications to their external surfaces. These range from some flaking of the external surface of the enamel to mild erosion of the fine surface details.

**MAK-VP-1/13 (Fig. 8e).** Left upper first molar. This specimen was found on October 15, 1990 during the sieving operation for MAK-VP-1/12. The crown is fractured and lacks its buccal and mesial faces. Portions of the enamel are root-etched.

**MAK-VP-1/83 (Fig. 8a).** Left mandibular ramus. This specimen was found by Alemu Ademassu on October 20, 1990. It was recovered in three major fragments that are accurately restored into one piece. The lateral end of the condyle is missing, the medial end is abraded, and the lateral surface of the ramus surface is mildly etched by root acids.

The comparative descriptions below focus on the MAK-VP-1/12 specimen because of its completeness. They are supplemented, where appropriate, by reference to the four other dental and mandibular specimens recovered from the Maka sands during the 1990 field season. The single upper tooth is described at the end. Tables 1 and 2 supplement the text and photographs. These provide metrics comparable to those previously published for the paratype series of *A. afarensis*.

## DESCRIPTIONS

The descriptions of the Maka remains are organized by tooth and element, not by individual specimen as presented above. Descriptions are for MAK-VP-1/12 except where noted.

### Dentition: macroscopic observations

#### Individual teeth.

**Lower lateral incisor.** The crown is worn to approximately the midcrown point, exposing a subrectangular dentine patch  $5.0 \times 1.4$  mm. In size, the incisor is near the *A. afarensis* mean. There is a slight lingual bevel to the occlusal platform. Lingual relief is minimal, closely matching the A.L. 333w-58 specimen.

**Lower canine.** The crown apex is worn to expose a 1.5 mm-diameter dentine patch. In labial (anatomically lateral) view the occlusal wear plane turns abruptly at midcrown, and the flat wear surface slants postero-inferiorly at approximately  $45^\circ$  toward the distal marginal tubercle. This angulation of the occlusal wear surface is also seen in L.H.-14, A.L. 333w-58, A.L. 198-1, and A.L. 400a. The often planar wear on the distal edge of *A. afarensis* lower canines is formed by contact with the mesial incisal ridge of the upper canine tooth (as seen in the A.L. 200-1a upper canine). In size, shape, and occlusal wear, the Maka canine is a close match for L.H.-14 and A.L. 400-1a, although

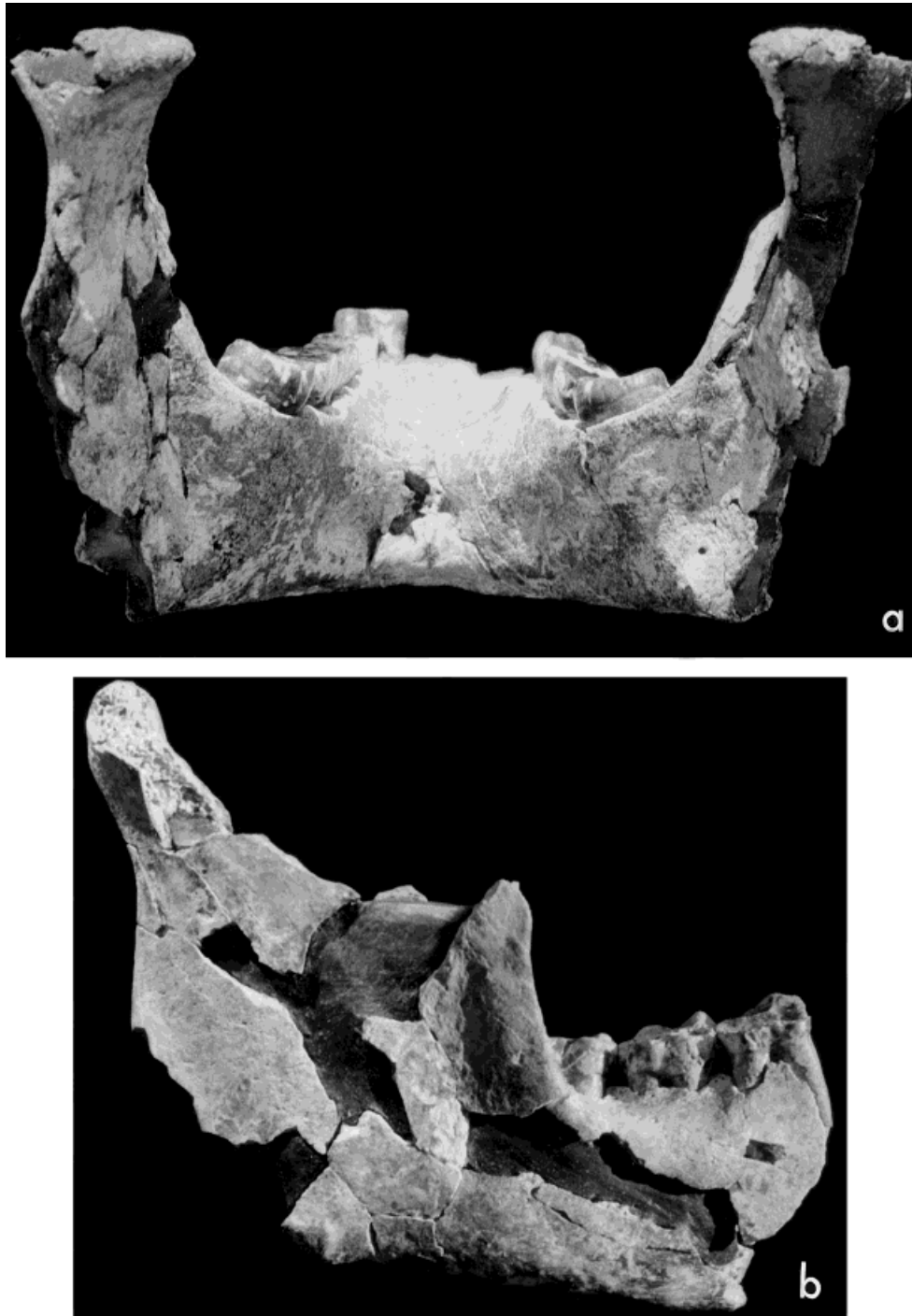


Fig. 4. **a:** MAK-VP-1/12, posterior view. **b:** MAK-VP-1/2, lateral view. Both natural size.

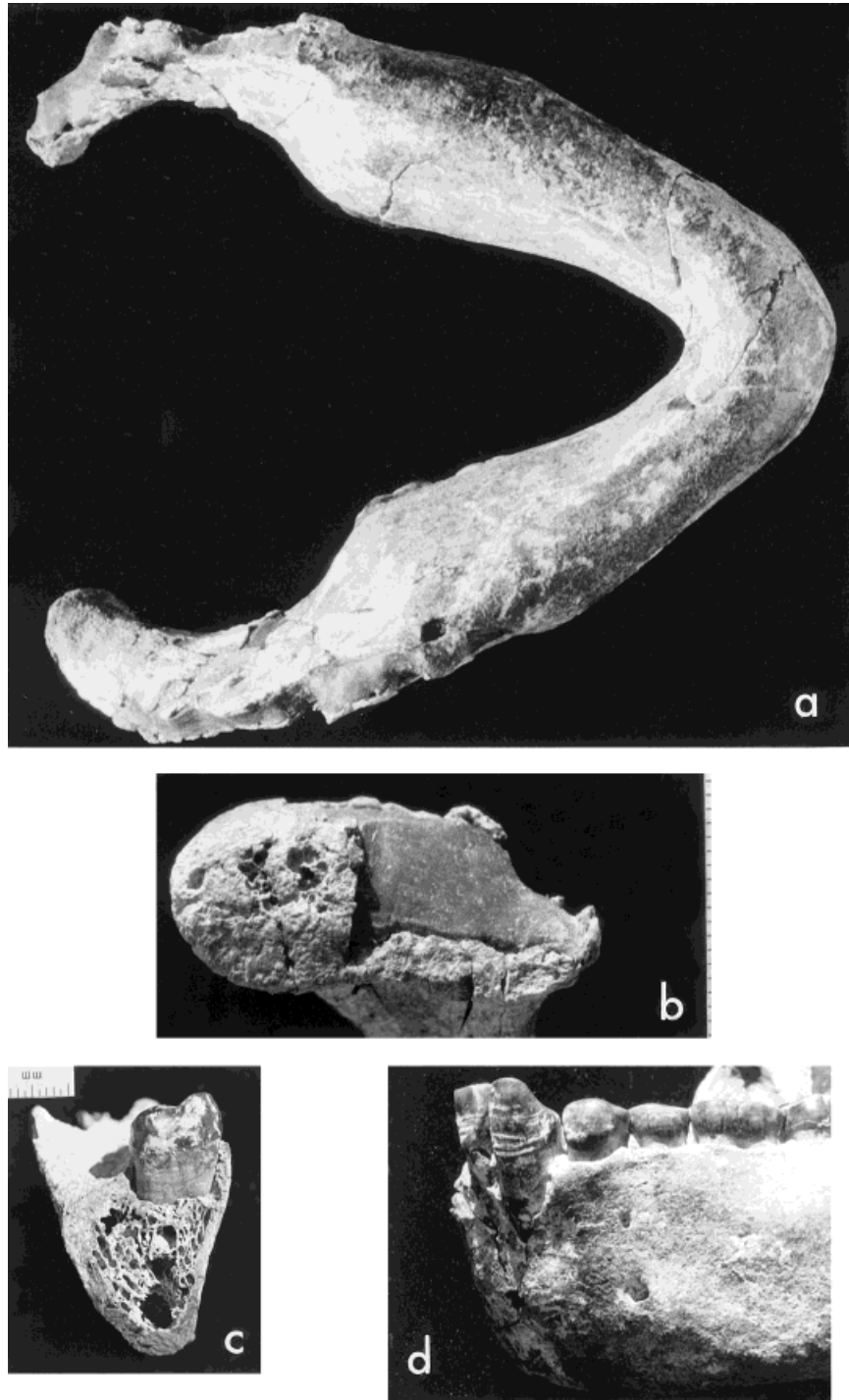


Fig. 5. MAK-VP-1/12. **a:** Basal view. **b:** Left condyle, superior view. **c:** Cross-sectional view. **d:** Lateral oblique view of canine "step." Natural size, except b and c scaled as shown (in millimeter increments).

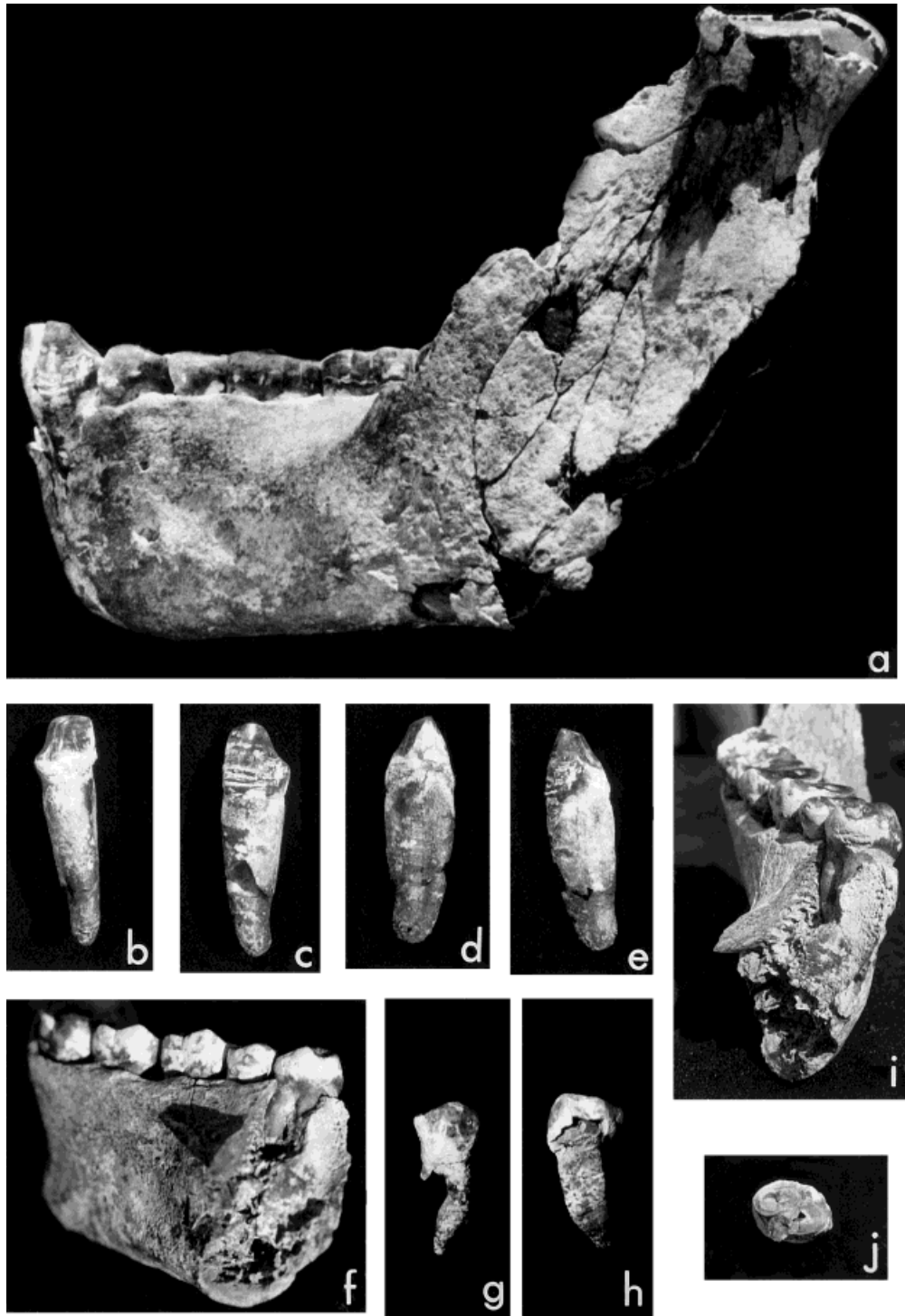


Fig. 6. MAK-VP-1/12. **a**: Lateral view. **b**: Left canine, lingual view. **c**: Left canine, buccal view. **d**: Left canine, mesial view. **e**: Left canine, distal view. **f**: Oblique view of exposed LP<sub>3</sub> root. **g**: RP<sub>3</sub>, buccal view. **h**: RP<sub>3</sub>, mesial view. **i**: Mesial view of exposed LP<sub>3</sub> root within broken mandible. **j**: Basal view of broken crown base of the RP<sub>3</sub>. Buccal at left, mesial at top. All natural size.



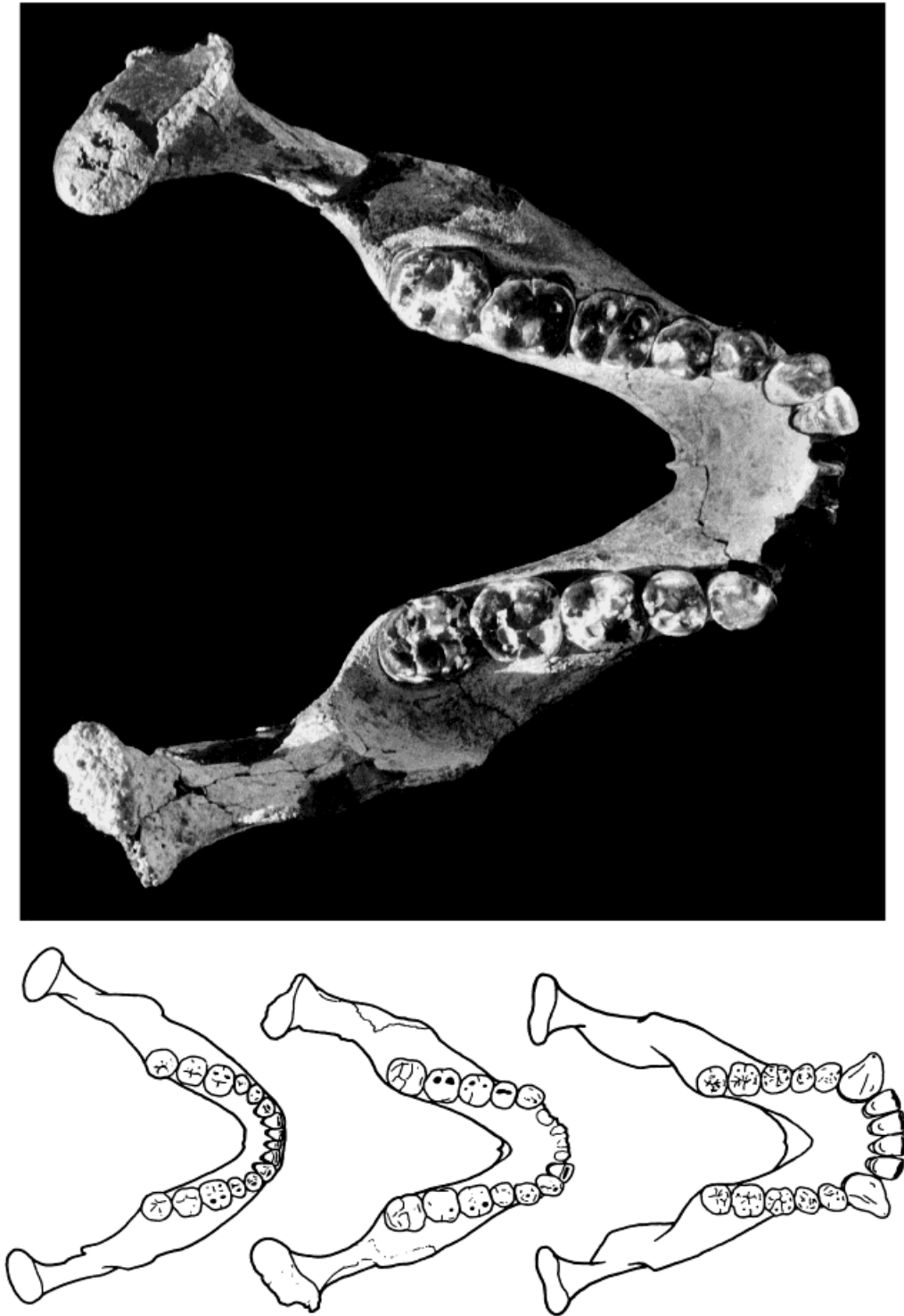


Fig. 7. MAK-VP-1/12. The mandible of *A. afarensis* (center) compared to a modern male common chimpanzee (right), and a modern human (left). Photograph natural size.

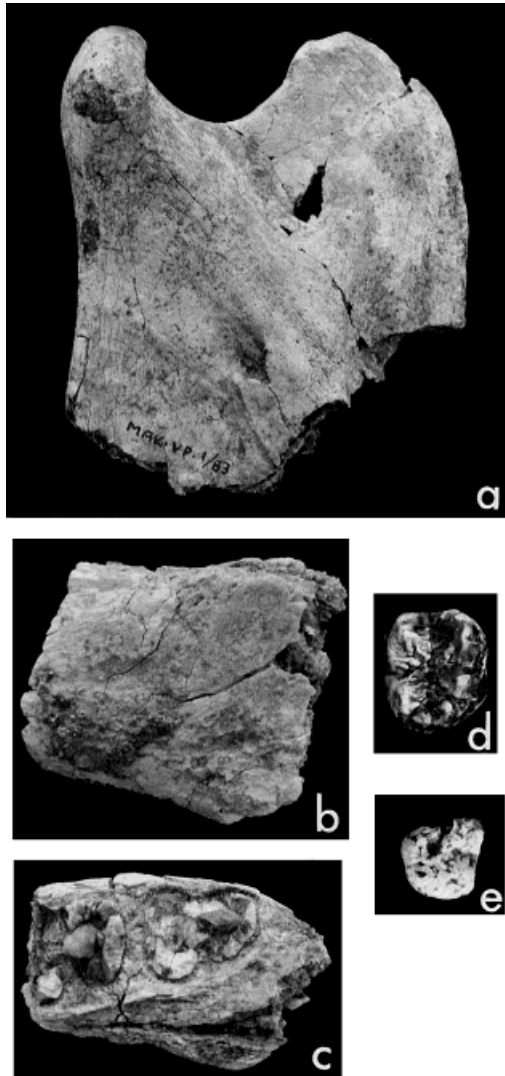


Fig. 8. Maka 1990 hominids. **a**: MAK-VP-1/83 ramus, lateral view. **b**, **c**: MAK-VP-1/6 mandible corpus, lateral and occlusal views, respectively. **d**: MAK-VP-1/4 lower molar. **e**: MAK-VP-1/13 upper molar. All natural size.

both of the latter specimens have greater lingual relief. There is a small, ca. 0.3-mm diastema between the canine and P3.

**Lower third premolar.** The left P3 is more heavily worn than the right and exhibits a circular, 0.4 mm diameter apical pit with exposed dentine atop the protoconid. The crowns are unequal in size, but near the *A. afarensis* mean (White et al., 1993). The metaconid is swollen and weakly separated

from the protoconid by a shallow fissure. The moderately defined anterior fovea at the mesiolingual corner of the crown is circumscribed by weak marginal ridges. Overall crown shape, anterior foveal development, and occlusal relief and wear are comparable to the Hadar A.L. 266-1, 333w-46, and 333-10 specimens.

Both right and left root systems consist of independent mesial and distal roots (Fig. 6). Both sides exhibit similar morphology, and detailed observation and measurement was possible on the right P<sub>3</sub> before mandibular assembly. The mesial root is plate-like, with a bucco-lingual breadth of 6.5 mm. It is set mesially and is only weakly oblique to the distal root, which is 8.4 mm in breadth. This root system approximates the "molarized" pattern considered by some to be characteristic of "robust" *Australopithecus* P<sub>3</sub>s (e.g., Wood et al., 1988). Such an incipiently molarized condition is also seen occasionally in other "nonrobust" taxa (OMO 18-33, KNM-ER 1814, STW 231/233, and STW 240). Natural fracture sections ca. 2–3 mm below the cervix reveal single root canals in both mesial and distal roots, with the distal canal elongated buccolingually.

**Lower fourth premolar.** The right P<sub>4</sub> is much more heavily worn than the left, with dentine exposed in an irregular 1.0–2.0 mm-wide trough down the buccal occlusal surface. Right and left crown sizes are asymmetrical, and near the *A. afarensis* mean. Shape and occlusal relief and wear are closely matched by the Hadar A.L. 266-1 and 400-1a and Laetoli L.H.-4 specimens.

**Lower first molars.** The right first molar is more worn distally, with dentin exposures on the protoconid (1.8 mm, circular), the hypoconid (2.2 diameter) and the hypoconulid (0.6 mm). Crown shape is square, and size is near the *A. afarensis* mean. The occlusal morphology and relief are similar to the Hadar A.L. 333w-60 and Laetoli L.H.-4 specimens. The slightly larger and more heavily worn M1 of the MAK-VP-1/2 individual is a good match for the Hadar A.L. 277-1 specimen, with which it shares a deep, cupped exposure of dentine on the buccal occlusal surface.

TABLE 1. Dental measurements<sup>1</sup>

	I <sub>2</sub>	C	P <sub>3</sub>	P <sub>4</sub>	M <sub>1</sub>	M <sub>2</sub>	M <sub>3</sub>	M <sup>1</sup>
Mesiodistal length								
Right								
MAK-VP-1/2					13.1 (13.6)	14.7 (15.0)	15.6	
MAK-VP-1/4							16.2	
MAK-VP-1/12			(9.7)	9.5 (9.7)	12.6 (13.0)	13.8 (14.2)	14.9 (15.2)	
Left								
MAK-VP-1/12	7.2 (w)	9.5	9.1 (9.3)	8.8 (9.0)	12.8 (13.1)	13.6 (14.0)	14.8 (15.3)	
MAK-VP-1/13								10.9
Buccolingual breadth								
Right								
MAK-VP-1/2					12.4	13.0	13.0	
MAK-VP-1/4							13.8	
MAK-VP-1/12			11.3 max	10.8	12.1	13.3	13.4	
Left								
MAK-VP-1/12	8.0	10.2 max	11.2 max	9.9	12.2	13.3	13.4	

<sup>1</sup> All measurements are in millimeters and follow techniques outlined in Johanson et al. (1982b). Estimates are in brackets. w, worn; max indicates maximum oblique buccolingual measure.

**Lower second molars.** The new Maka sample comprises four second molars, the first two of which are from MAK-VP-1/12. Crown size of the latter is near the *A. afarensis* mean. Crown wear on this specimen is highly asymmetric, with far more dentine wear exposure on the right M<sub>2</sub> at both the protoconid and hypoconid positions (deep, pitlike exposures of 3.2 mm diameter and 2.6 mm, respectively). In size, shape, and wear, the right second molar is similar to Hadar A.L. 333w-59 and the left is a fair match for L.H.-4. The larger, more heavily worn second molar of the MAK-VP-1/2 individual bears a deep, extensive dentine wear exposure on the hypoconid/hypoconulid and protoconid. Its overall crown shape, size, and wear are similar to the Laetoli L.H.-23 M<sub>2</sub>. The largest of the three Maka individuals at the M<sub>2</sub> position is MAK-VP-1/4. This slightly worn crown is slightly narrower and longer than the A.L. 277-1 specimen's M<sub>2</sub>. A.L. 277-1 is at the high end of the *A. afarensis* M<sub>2</sub> size range.

**Lower third molars.** The MAK-VP-1/12 third molars are nearly equally worn, without enamel perforation. The MAK-VP-1/2 individual displays a more heavily worn right M<sub>3</sub>, which also lacks dentine exposure. It is slightly larger. The Maka specimens are near the *A. afarensis* mean in crown size. In size and shape, the Maka specimens lie between L.H.-4 and A.L. 333w-57.

**Upper first molar.** The MAK-VP-1/13 specimen is broken, but its mesiodistal dimen-

sion is the smallest known for *A. afarensis*. It bears a deep, bilobed protocone dentine exposure that extends from the protocone to the mesial marginal ridge.

### Overall dentition.

**Macroscopic wear.** The MAK-VP-1/12 specimen exhibits the typical *A. afarensis* occlusal and interproximal wear pattern, in which there is a strong wear gradient combined with retained cusp saliency. The wear gradient is similar to that seen on the A.L. 288-1 and L.H.-4 specimens. The extent of wear on the Maka dentition is intermediate between these. The Maka postcanine rows show strong occlusal relief relative to other *Australopithecus* species, with sharp, occlusally projecting metaconid and entoconid edges. The marked asymmetry of occlusal wear (particularly on the P<sub>4</sub>) is possibly related to the degenerative changes on the mandibular condyles (see below). The MAK-VP-1/2 specimen was an older individual with a steep molar wear gradient.

**Proportions.** The proportions between anterior and posterior teeth are very similar to those seen in other specimens of *A. afarensis* from both Hadar and Laetoli (Fig. 11).

**The C/P<sub>3</sub> complex.** The distal incisal edge of the MAK-VP-1/12 lateral incisor is level and continuous with the worn mesial incisal ridge of the canine, as it is in the A.L. 400-1a specimen. However, unlike the A.L. 400 specimen, the Maka specimen shows a steep "drop" of the occlusal edge across the poste-

TABLE 2. Mandible measurements<sup>1</sup>

At crowns Between crowns	I <sub>1</sub>	I <sub>2</sub> I <sub>1</sub> /I <sub>2</sub>	C I <sub>2</sub> /C	P <sub>3</sub> C/P <sub>3</sub>	P <sub>4</sub> P <sub>3</sub> /P <sub>4</sub>	M <sub>1</sub> P <sub>4</sub> /M <sub>1</sub>	M <sub>2</sub> M <sub>1</sub> /M <sub>2</sub>	M <sub>3</sub> M <sub>2</sub> /M <sub>3</sub>
Perpendicular corpus height								
Right, at crowns								
MAK-1/12	x	x	x	(33.0 ± 0.5)	31.3	29.7	(27.7 + 1)	(28.2 + 1)
MAK-1/2							32.6	30.7
Right, between crowns								
MAK-1/12	x	x	x	(36.7 ± 0.5)	34.5	31.8	29.2	(27.2 + 1)
MAK-1/2							34.6	31.8
Left, at crowns								
MAK-1/12	x	x	(34.4 ± 1)	33.7	33.6	31.3	31.1	33.9
Left, between crowns								
MAK-1/12	x	x	x	34.8	34.1	33.0	31.0	32.0
Minimum corpus breadth								
Right, at crowns								
MAK-1/12	21.6	x	20.9	19.6	18.2	18.8	20.8	Ramus
MAK-1/2						19.6	21.4	Ramus
Right, between crowns								
MAK-1/12		21.2	20.8	20.5	18.5	17.8	20.2	25.4
MAK-1/2							20.2	23.6
Left, at crowns								
MAK-1/12	21.4	20.5	20.6	18.6	17.2	18.6	20.3	Ramus
Left, between crowns								
MAK-1/12		21.4	20.5	19.2	17.8	17.4	18.9	23.9
Various metrics, MAK-VP-1/12								
Bi-internal alveolar margin breadth:								
I <sub>1</sub> , 4.6; I <sub>2</sub> , 11.6; C, 20.4; P <sub>3</sub> , 26.7; P <sub>4</sub> , 29.5; M <sub>1</sub> , 31.5; M <sub>2</sub> , (35 ± 1); M <sub>3</sub> , (43 ± 1)								
Bi-crown center breadth:								
C, (30 ± 1); P <sub>3</sub> , 35.8; P <sub>4</sub> , 38.0; M <sub>1</sub> , 42.0; M <sub>2</sub> , 44.4; M <sub>3</sub> , 50.3								
Maximum bicondylar breadth (118 ± 2)								
Minimum bicondylar breadth 68.2								
Mental foramen height 1.9; 1.0 (R) (multiple); 1.6; 1.0 (L) (multiple)								
Mental foramen length 2.6; 1.0 (R) (multiple); 3.8; 1.3 (L) (multiple)								
Minimum height, base of mental foramen to basal contour 16.4 (R) (multiple); 15.3 (L) (multiple)								
Minimum height, base of mental foramen to alveolar margin 18.4 (RP <sub>4</sub> ) (multiple); 19.1 (R) (multiple)								
Top condyle to basal plane (76 ± 2) (R); (77 ± 2) (L)								
Maximum mandibular length (120 ± 2)								
Maximum condylar breadth (M-L) 31.7 (L)								
Maximum condylar length (A-P) (15) (L; pathological)								
Bi-mental foramen breadth (anterior edge) 40.3								
Height of condyle above occlusal plane (I <sub>1</sub> -M <sub>3</sub> ) (47 ± 2) (R); 42 (L)								
Various metrics, MAK-VP-1/2								
Minimum anteroposterior ramus length 52.4								
Height of condyle above occlusal plane (M <sub>2-3</sub> ) (63 ± 2)								
Various metrics, MAK-VP-1/83								
Minimum anteroposterior ramus length 58.6								

<sup>1</sup> All measurements are in millimeters and follow techniques outlined in White and Johanson (1982). Estimates are in parentheses. x, broken.

rior surface of the canine (Fig. 5d). In other words, there is a marked "step" or "drop-off" from the higher incisal/anterior canine edge to the lower occlusal surface of the third premolar. This would also have been the case for L.H.-4 as well as for many of the other *A. afarensis* mandibles. This is very different from the condition in apes, where the incisor and premolar occlusal surfaces both lie inferior to the level of the canine apex. In humans and other species of *Australopithecus*, the occlusal surfaces of all three crowns are at about the same height. The MAK-VP-1/12 specimen shows a small gap between the left C and P<sub>3</sub>, and there are no

interproximal facets on the distal C or mesial P<sub>3</sub> crown faces. Diastema are common in *A. afarensis*, previously recorded in approximately half of the available sample.

*Microscopic wear and enamel thickness.* Occlusal and interproximal wear are present on all of the teeth. Although not formally studied, the molar occlusal microwear is dominated by long, buccolingually oriented striae. Very few pits or mesiodistally oriented striae are observed. This is more similar to wear patterns described for *A. africanus* than *A. robustus* (dominated by pits) (Kay and Grine, 1988). Additional stud-



ies of *A. afarensis* microwear beyond those of Ryan and Johanson (1989), Greenfield (1990b), Puech et al. (1983, 1986), and Puech and Albertini (1983, 1984) are needed.

Enamel thickness can be measured at either the occlusal surface or points of fracture (here limited to the cervical margins, far less informative about overall enamel thickness than measurements at the occlusal surface). Both the canine and the incisor lend themselves to occlusal surface measurement better than the molars. In molars, estimation of enamel thickness using occlusally exposed dentine is complex due to uncertainty about the topography of the dentin-enamel junction and erosion of the enamel. The best way to measure molar enamel thickness is in broken or sectioned specimens.

In the Makà right P<sub>4</sub>, the advanced wear allows assessments of coronal enamel thickness at the MB (1.7 mm) and DB (1.3 mm) corners of the crown. In the canine, the thickness along the labial face can be measured near the crown apex cusp, where it has a thickness of ~1.6 mm. The enamel is substantially thinner on the lingual and distal sides. Minor attrition has thinned the enamel somewhat at these locations. Chimpanzees in a limited sample do not exceed 0.7–0.9 mm thickness in similar labial locations. Humans characteristically have enamel on the labial C surface of greater than 1 mm in a homologous location.

The significance of these enamel thickness values on the Makà and other *A. afarensis* specimens is that selection for increase in enamel thickness in the molars and premolars (the dietarily significant dimension) may have resulted in a systemic increase in enamel thickness in the anterior teeth. This is especially the case for the occlusal surface enamel.

#### Dentition: microscopic and developmental observations

**Surface topography.** The excellent preservation and nearly full complement of permanent teeth afford an opportunity to address issues of dental histology and development for the MAK-VP-1/12 specimen. The teeth were examined by binocular microscope and the surface details by scanning electron microscopy (SEM) on epoxy

positives. There is a "stair-step" morphology produced by the flaking of enamel along the outermost planes of the striae of Retzius (SOR). There is also minor erosion of the surface, perhaps due to postdepositional etching.

Perikymata were visible on all teeth. They exhibit the characteristic morphology of human perikymata of an increasing density towards the cervical margin. No tooth yielded a complete cusp to cervix count of perikymata. Occlusal wear and polishing obliterated the most cuspal perikymata. Crown formation periods could not be estimated using this approach. The perikymata follow an expectedly sinusoidal path in the cervical areas.

In the lateral incisor, the perikymata density increases from cusp to cervix, indicating a slowing of growth as the cervix was reached. This is similar to other *A. afarensis* teeth and contrasts with the regular cusp to cervix spacing seen in robust *Australopithecus* incisors (Bromage and Dean, 1985; Beynon and Dean, 1988). For Makà, the density of perikymata markedly increases per mm of height (10 per 1.4 mm to 10 per 1.0 mm) in the area where the labial and lingual extensions bifurcate. This is also seen in L.H.-2 (Beynon and Dean, 1988). This pattern suggests that modifications of the growth parameters (especially duration) occur at the more developmentally plastic cervical portion rather than at the cuspal portion (Simpson et al., 1990; Simpson and Kunos, 1998; Reid et al., 1998a,b).

**Pathology and development.** The MAK-VP-1/12 dentition exhibits evidence of pathological growth. The RP<sub>4</sub> has a macrochip with rounded edges whose origin is indeterminate. Like some other *A. afarensis* individuals (Johanson et al., 1982b), the Makà specimen has multiple enamel surface defects. The lateral incisor and the canine both have three major transverse surface defects on their labial enamel surfaces, each with multiple identifiable perikymata in their troughs. The right M<sub>1</sub> has a single, thin, cervically located band. Shallow transverse striae are also visible on the P<sub>4</sub> and the other molars.

Based on the number of perikymata in each defect, it is possible that the most

## RELATIVE DENTAL MATURATION - C with I2

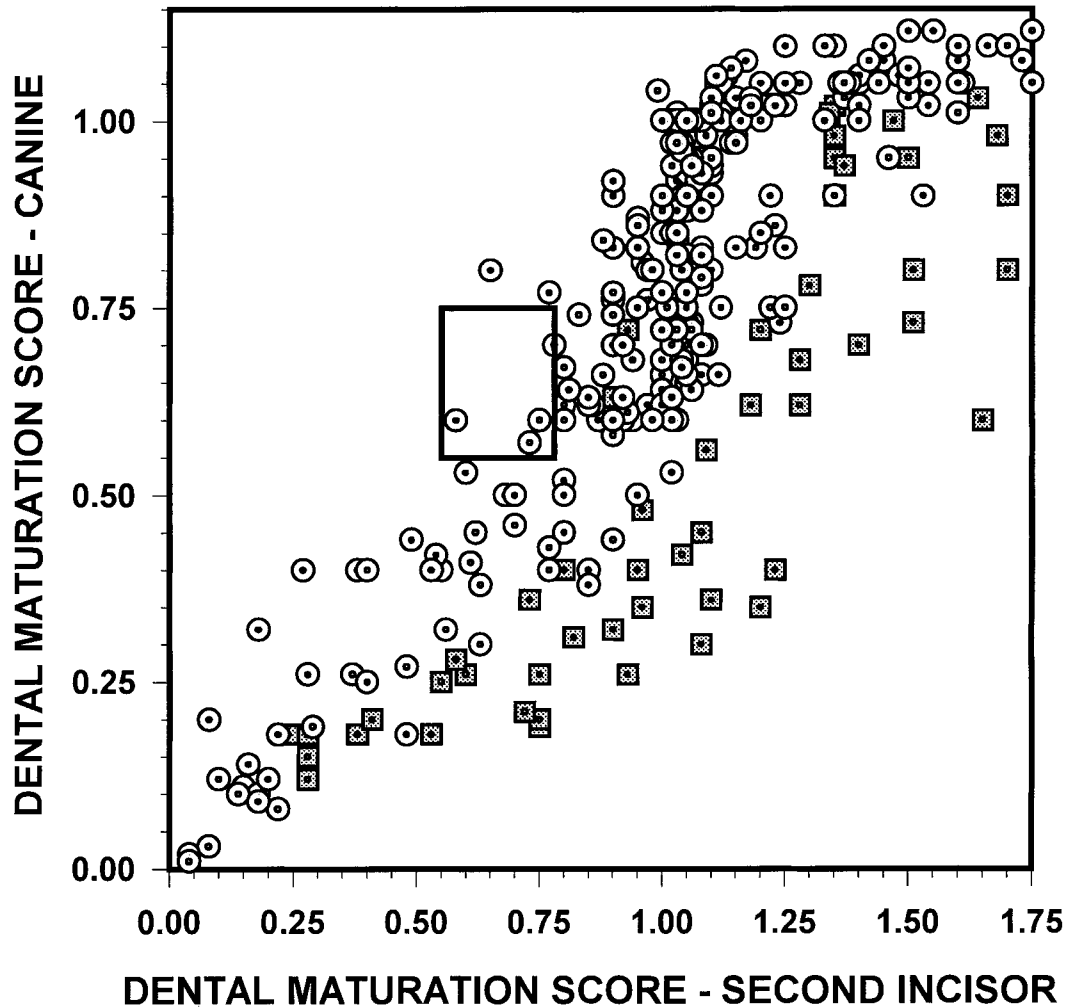


Fig. 9. Bivariate comparison of the development of the mandibular canine and lateral incisor. On a scale of 0.00–2.00, 0.00 equals no evidence of crown, 0.50 equals enamel crown one-half complete, 1.00 equals crown complete with no root formation, etc. Open circles,

humans; gray squares, African apes; large open box, MAK-VP-1/12. Box includes full range of possibilities for registering the hypoplastic bands. Note that the relative growth of the MAK-VP-1/12 canine is derived towards a more human ontogenetic pattern.

cuspal defect on the Maka canine is a product of the same episode as the one located most cervically on the lateral incisor. If we assume that this match is valid, the pattern of dental growth in the Maka specimen may be compared (Fig. 9) with developmental data from a large series of humans ( $n = 422$ ) and African apes ( $n = 99$ ) (Simpson et al., 1990, 1992; Simpson and Kunos, 1998).

MAK-VP-1/12 shows a reduced canine crown and an earlier development of the canine relative to the lateral incisor than in the extant apes. The earlier, more prognathic *Australopithecus* species, *A. afarensis* and *A. africanus*, are intermediate in their pattern of dental development between the African apes and the more orthognathic hominids (*A. robustus*, *A. boisei*, *H. sapiens*).

Not only had *A. afarensis* reduced the size of the canine, it also appears to have changed its relative ontogenetic pattern (Simpson et al., 1990, 1992). It appears that in *A. afarensis* the large canine no longer played a central role in the acquisition or maintenance of social rank or reproductive success. (Johanson and White, 1979; Lovejoy, 1981).

### The mandible

Previous comparative assessments of the *A. afarensis* mandible figured prominently in the recognition and systematic assessment of the taxon (Johanson et al., 1978; Johanson and White, 1979; White et al., 1981). The four new Maka specimens do not extend the mandibular size range of known *A. afarensis*. The most complete, MAK-VP-1/12, is almost exactly the same size as the holotype L.H.-4 specimen (Table 2). The ramus fragment MAK-VP-1/83 is also an appropriate size match for these. The small fragment MAK-VP-1/6 is at the small end of the *A. afarensis* range in corpus dimensions at  $M_2/M_3$ . The largest of the Maka specimens, MAK-VP-1/2, is still considerably smaller than the largest *A. afarensis* specimens from Hadar.

Bony morphology of all four specimens is well within the established *A. afarensis* ranges in all features (Figs. 10, 12, 13), but as for the teeth (Fig. 11), the completeness of the Maka specimens allows them to add valuable information about that species.

### Mandible corpus.

**Occlusal aspect.** The overall shape of the dental arcade is almost exactly like A.L. 400-1a and L.H.-4. The postcanine tooth row is straight. Incisors and canines are vertically implanted in a tight arc, contrasting strongly with the procumbent incisors of most African apes.

**Lateral aspect.** Both Maka specimens deepen slightly anteriorly, as do most *A. afarensis* mandibles. The lateral prominence is difficult to assess in the MAK-VP-1/2 specimen, but is moderate in MAK-VP-1/12. This feature is highly variable in *A. afarensis*. The relative placement and morphology of the ramus root/corpus junction

was the most poorly understood area of the *A. afarensis* mandible prior to the new Maka specimens. In a true lateral view, the rami obscure the entire third molar crowns of both new specimens. This is very different from the ape condition where the ramus arises more posteriorly, usually obscuring less of the third molar, even in the gorilla. This anteriorly arising, vertically oriented ramus was indicated on the broken Hadar adults (except for A.L. 198-1) and was pre-saged by the immature 333-43 specimen. This young individual, with both deciduous molars in place, shows that even early in ontogeny the *A. afarensis* ramus was anteriorly placed, large, and robust compared to that of extant apes. In addition to the anterior position of the ramus root, a substantial extramolar sulcus (the anterior ramus edge is set 13 lateral to the buccal anterior  $M_3$  crown) is present on both Maka individuals.

A distinguishing feature of *A. anamensis* and *A. afarensis* mandibles is the lateral corpus contour hollow, framed by the swollen alveolar region above, by the root of the ramus behind, and inferiorly by the basal marginal torus sweeping upward to join the  $C/P_3$  root jugae antero-inferiorly. The mental foramen is usually set at the antero-inferior corner of this hollow, which varies in depth among described *A. afarensis* mandibles. Both of the new Maka mandibles that preserve this area display this lateral corpus contour hollowing. It is intact on both sides of MAK-VP-1/2 where its extent, depth, and a-p elongate shape are near the *A. afarensis* mean, approximating the hollows on the A.L. 198-1 and A.L. 400-1a specimens.

The mental foramen is multiple on both sides of the MAK-VP-1/12 specimen. As gauged perpendicular to the alveolar margin of the  $P_3-M_1$  series, the foramen is centered below midcorpus at the  $P_3/P_4$  position. As in most other *A. afarensis* specimens, the foramen opens antero-superiorly, toward the midcanine crown. A single accessory foramen is set midway between the major mental foramen and the alveolar margin on both sides, strongly recalling the situation in L.H.-4.

As in other *A. afarensis*, the lateral to anterior corpus transition is accomplished across an even curve to which both the C and

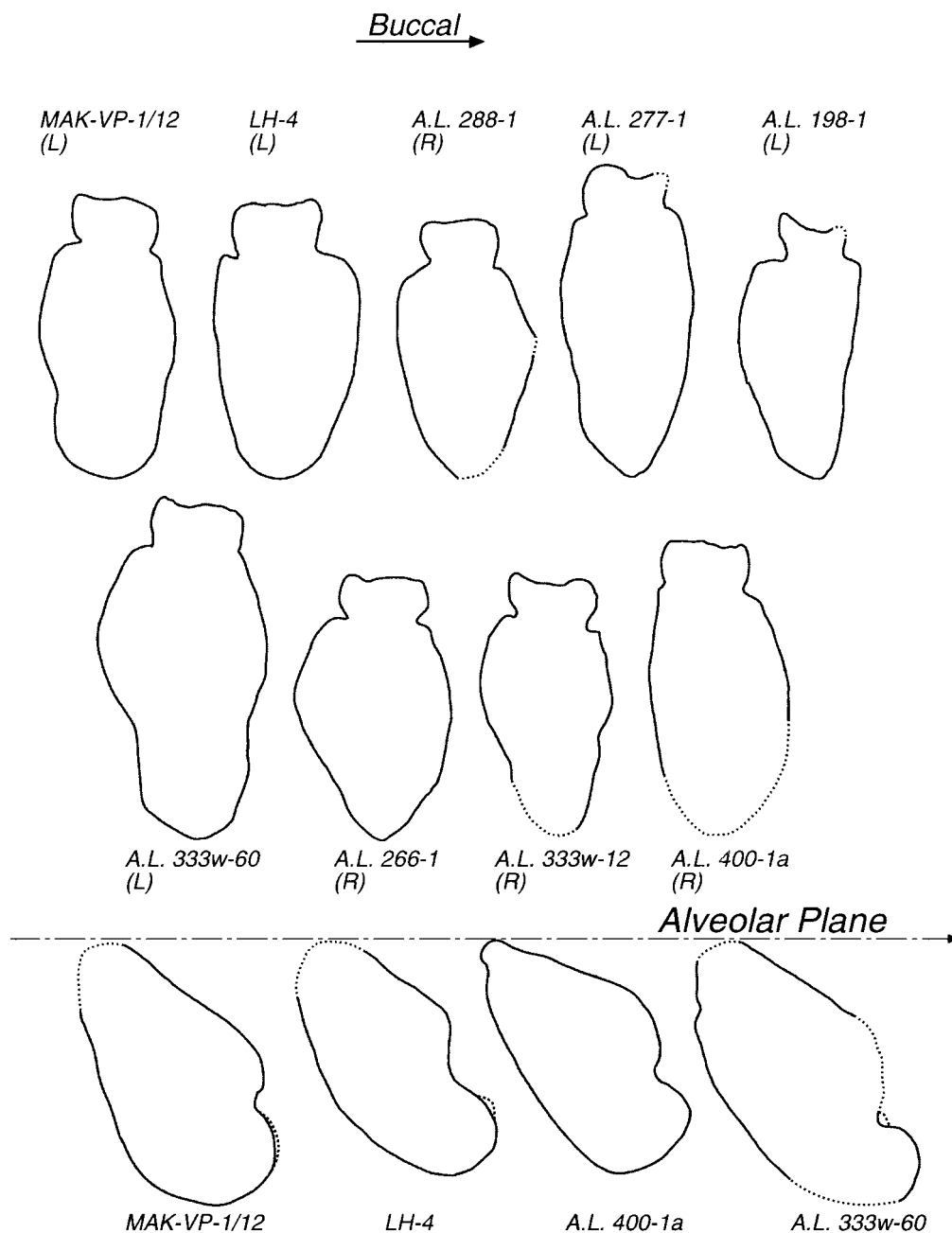


Fig. 10. Mandibular corpus cross sections. Upper two rows are sections taken through casts at the first molar midcrowns, perpendicular to the lingual alveolar margins. The lower sections were taken through the midlines, with the sections oriented relative to the

alveolar row. Broken portions and mental spines indicated by dotted lines. Note similarity of the Maka and Laetoli holotype specimens in shape and size, and the placement of these individuals within the range of *A. afarensis* mandibles from Hadar.

$P_3$  roots contribute. This is very different from the condition in apes, where the canine jugum is the dominant, and often more abrupt, turning point. Platysmatic striae

are seen on both Maka specimens, and those on MAK-VP-1/12 are similar to those on the Hadar A.L. 288-1 mandible in prominence, orientation, and position.



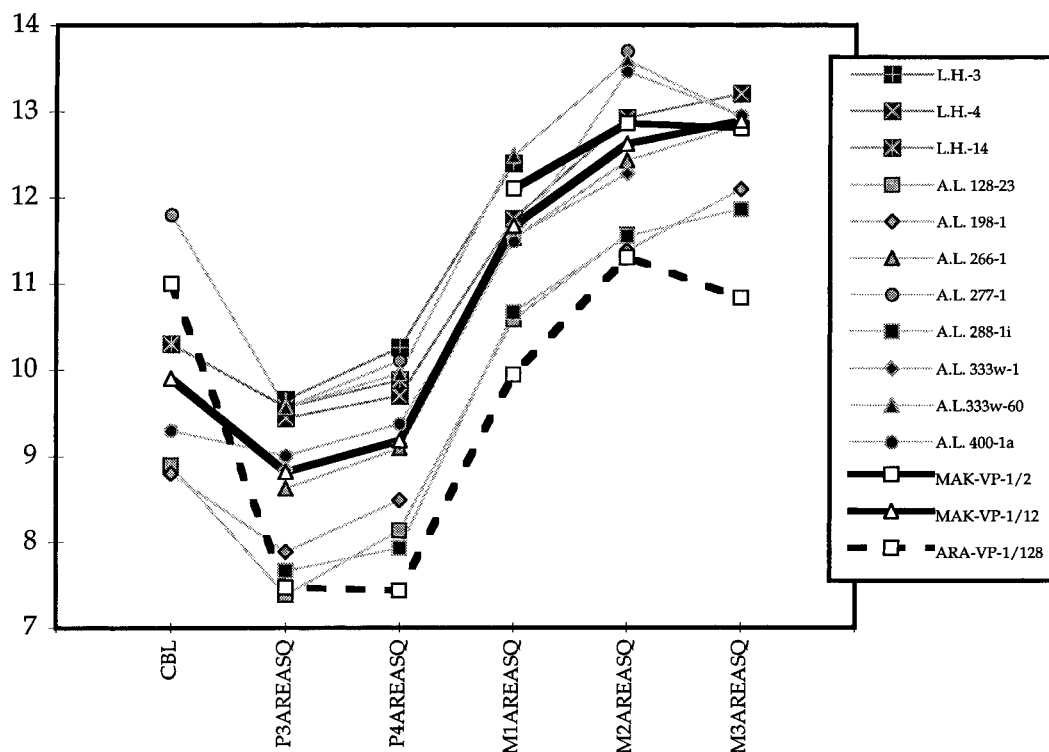


Fig. 11. Dental size and proportions in *Australopithecus afarensis* and *Ardipithecus ramidus*. All published specimens from Hadar/Laetoli sufficient to show relative dental proportions are depicted (specimens with at least three measured canine or postcanine teeth). Note that MAK-VP-1/12 has dental proportions typical for *A. afarensis*, and at midsize range. The *Ardipithecus ramidus* dental set (White et al., 1994) shows small postca-

nines, especially  $P_4$  thru  $M_3$ , and a relatively large canine. Postcanine dimensions are the square root of measured crown area, with estimates made allowing for partial crown damage when appropriate. Measured crown areas were taken from Suwa (1990) and Suwa et al. (1994), or measured in the present study following the same methods. Canine dimension is buccolingual breadth.

**Medial aspect.** The alveolar prominence is not marked in either specimen, and the basal portion of the medial corpus is only weakly hollowed in the subalveolar region. This is a highly variable feature in *A. afarensis*. The disposition of the mylohyoid line is also typical for *A. afarensis* on both Maka specimens.

**Anterior symphyseal region.** In true lateral view, the angulation and shape of the midline profile of the mandible's anterior symphyseal region have come under recent scrutiny with the announcement of two new species of *Australopithecus* (Leakey et al., 1995; Brunet et al., 1996). The range of variation in this feature in modern chimpanzees is great, from a subvertical, flat alveolar region with a bulbous base, to more evenly angled, posteriorly raking profiles. Similar variation is also seen in the gorilla.

The more vertically implanted the incisors, the more vertical the alveolar portion of the symphysis tends to be. Variation in shape and slant of this region is also substantial among early hominids, ranging from the A.L. 288-1 specimen (fairly vertical, evenly rounded) to the L.H.-4 mandible (superiorly vertical, sharply sloping inferiorly, creating a "bulbous" symphysis). The new Maka specimen is similar to the A.L. 288-1 specimen in these features (particularly in the subincisal jugae region), but at a larger size, and with a slightly more posterior slant. It is narrower than the A.L. 400-1a specimen, but its basal half does not slope as strongly posteriorly as does L.H.-4.

At the break between the alveolar and basal portions of the midline contour there is a low, rounded, palpable eminence that occupies the symphyseal tuber position. This

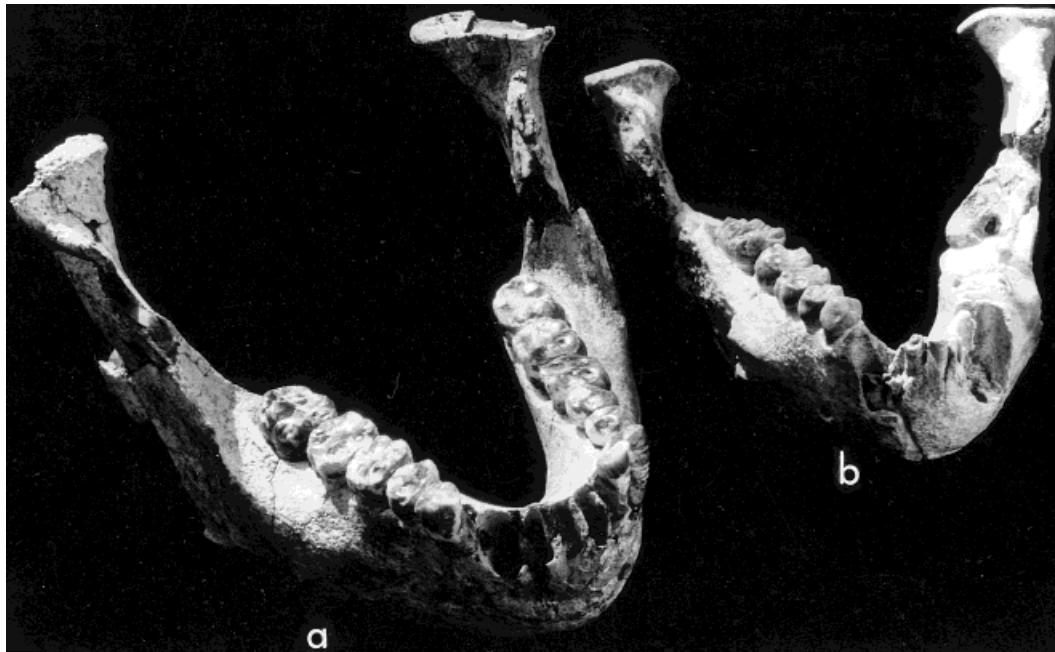


Fig. 12. Oblique view of the MAK-VP-1/12 (a) and the A.L. 288-1 ("Lucy") (b) mandibles of *A. afarensis*.

is similar to, but placed more inferiorly than that seen in the L.H.-4 mandible. The basal incisura is not so marked as in L.H.-4 because the inferior anterior marginal tubercles are not so prominently developed.

**Posterior symphyseal region.** The postincisive planum of MAK-VP-1/12 is deeply hollowed, both transversely and supero-inferiorly. This area is slightly narrower here than in L.H.-4, but wider than in A.L. 288-1. It is very similar to what is seen in A.L. 400-1a. The superior transverse torus and the genioglossal fossa, whose superior boundary it forms, are developed in Maka to the same extent as in L.H.-4. In true occlusal view the torus extends posteriorly to the anterior  $P_4$  position, as seen in most other *A. afarensis* specimens. The supraspinous foramen of MAK-VP-12/1 perforates the floor of the genioglossal fossa, surmounting a vertical bony septum that bisects the fossa and is continuous inferiorly with a prominent, single bony spine. This differs from the L.H.-4 arrangement only in the narrowness and prominence of the single mental spine. The inferior transverse torus is similar in

size, shape, and disposition, but in the Laetoli specimen it extends more posteriorly relative to the superior transverse torus because of the more receding nature of the basal portion of its symphyseal area.

**Basal aspect.** The basal aspect of the Maka specimen is similar to that of A.L. 288-1 in shape. It is not so posteriorly everted as in the L.H.-4 specimen, largely because of the latter's more posteriorly extending inferior transverse torus. Digastric fossae are small and shallow when compared to the extensive scalloping on the A.L. 400-1a base below the inferior transverse torus.

#### **Mandible ramus.**

**Lateral aspect.** The three new Maka specimens confirm that the *A. afarensis* mandibular ramus was vertically disposed, anteriorly placed, tall, and robust compared to that in chimpanzees. These features are apparent even in comparisons of very young *A. afarensis* individuals (A.L. 333-43). The MAK-VP-1/2 ramus is the largest, and is as tall and wide as the large, very similar A.L. 333-108 from Hadar. The coronoid process of



Fig. 13. Reconstructed mandibular bodies of the most complete mandibles from the three major *A. afarensis* sites. **Top:** Maka MAK-VP-1/12. **Right:** Laetoli L.H.-4. **Left:** Hadar A.L. 400-1a. Alignment of the specimens in this nonstandard orientation facilitates comparisons of dental size and arcade shapes. It is

difficult to find individuals whose dental arcades match so closely in contemporary populations of African apes, lending strong support to the interpretation of *A. afarensis* as a single, ecologically and geographically widespread early hominid species.

MAK-VP-1/83 is very broad and similar to the A.L. 333-100 specimen from Hadar in all details, including the lack of lateral flare and marked temporalis rugosity. The ectocondyloid buttress is weak in all three specimens. There are very strong but broken ectoangular tuberculi on both MAK-VP-1/12 and MAK-VP-1/2. Preserved portions of gonial angle on both show that this part of the ramus was fairly vertical and framed by these masseteric attachments, neither inverted nor everted, but with a moderate masseteric fossa within the frame.

*Medial aspect.* The medial surface of the ramus of both Maka specimens shows very large tuberosities for the medial pterygoid muscles that encroach well onto the ramus. There is a deep excavation in the area of the triangular planum on MAK-VP-1/2, similar to that seen on the A.L. 333-100 specimen. The MAK-VP-1/83 endocondyloid buttress is more salient than the low but rugose endocoronoid process. The former structure demarcates the perpendicular transition from the area antero-inferior to the condyle to the medial surface of the ramus. The expansive



Fig. 14. Lateral radiographs of MAK-VP-1/12. **Top:** Right corpus. **Bottom:** Left corpus. Approximately natural size.

surface between the Maka specimen's endo-coronoid buttress and the anterior edge of the ramus is rugose, with the proportions and relief in this region very similar to those seen in A.L. 333-100. The wide bony area anterior to the buttress sets *A. afarensis* apart from extant apes. The retromolar fossa is extensive in both Maka specimens, bounded laterally by the sharp ramus root that is already distinct at a vertical position at the level of the alveolar margin. The mandibular foramen exits postero-superiorly behind the retromolar fossae, into a sulcus that extends nearly to the posterior ramus margin below the condyle.

*Mandibular condyles.* All three new Maka specimens preserve portions of the condyle.

The MAK-VP-1/12 specimen is arthritic and is further described below. The MAK-VP-1/2 condyle is broken in half, but was evidently in the midportion of the known *A. afarensis* size range. This condyle, as well as that of MAK-VP-1/83, is very similar in articular coverage and size to A.L. 333w-16.

#### Bony pathology

The only clearly pathological condition seen on the new specimens involves the mandibular condyles of MAK-VP-1/12. The better-preserved left condyle shows severe joint degeneration, with a very rough, irregular, pitted subchondral surface. This is the earliest bilateral temporomandibular joint disease documented among hominids. It may



be the cause or consequence of the morphological and occlusal wear asymmetries described above for this individual.

### Radiography

Both MAK-VP-1/12 and MAK-VP-1/2 specimens reveal subocclusal morphology consistent with previous descriptions of Hadar *A. afarensis* mandibles (Ward et al., 1982; Fig. 14). The mandibular canal can be seen to pass above the distal  $M_3$  root apex, curve downward to reach its lowest position below  $M_1$ , and then curve upward to reach the mental foramen at the  $P_3/P_4$  position. The distance between the  $M_1$  root apex and the mandibular canal is greater in the MAK-VP-1/2 mandible, possibly related to the more heavily worn  $M_1$  crown and presumed continuous eruption. Of note are the double-rooted right and left  $P_3$ 's with subequal mesial and distal root canal dimensions, and the single-rooted  $P_4$  on both sides. The root canal is singular on the right  $P_4$ , whereas a smaller distal canal furcation occurs on the left side at midroot height.

### DISCUSSION

The new specimens from Maka are very similar in all respects to the paratype series from Hadar and Laetoli. They do not significantly extend the known metric or morphological ranges for this species, except perhaps in mandibular premolar root form. However, the preservation of the Maka mandibles allows them to contribute significantly to systematic and functional considerations of *A. afarensis*.

#### The *A. afarensis* mandible

The mandible and its dentition played critical roles in the original description of *A. afarensis*. The Laetoli L.H.-4 specimen was chosen as the holotype of this taxon (Johanson et al., 1978). Primitive dental and mandibular characters were used to distinguish *A. afarensis* from other early hominids. The functional dentognathic morphology of this species, described as unique, has been further elucidated by additional discoveries over the last 20 years, culminating with the recovery of a large adult male skull of the species that includes the largest known mandible of *A. afarensis* (Kimbel et al., 1994). This discovery confirms earlier interpreta-

tions of the cranial morphology of the species (Kimbel et al., 1984).

The Maka MAK-VP-1/2 individual was probably a male, based on its position towards the large end of the overall species range. The more complete but smaller MAK-VP-1/12 individual is nearer to the *A. afarensis* mean size, and its sex cannot be reliably determined. Descriptions of the large series of mandibles and teeth recovered from the slightly younger Hadar site to the immediate north (Kimbel et al., 1994) will be crucial in clarifying the nature of mandibular and dental variation in this species.

With the discoveries of *A. anamensis* and *A. ramidus*, *A. afarensis* is no longer the most primitive fossil hominid. This new perspective is an important one for both phylogenetic and functional studies. All three of the new Maka mandibles reveal a primate with a unique masticatory apparatus. *A. afarensis* differs from all extant apes and the more primitive *Ardipithecus* in the relatively small size of its canines, and its relatively large, thick-enamelled postcanine dentition. Relative to the chimpanzee, *A. afarensis* mandibles feature tall, vertically oriented rami positioned anteriorly relative to the dentition. Relative to the chimpanzee, *A. afarensis* mandible bodies are more robust and the postcanine chewing platform is enlarged, with thicker enamel. This already megadont taxon, and perhaps its closely related temporal precursor *A. anamensis*, represent initial functional steps that would eventually culminate in the far more derived, specialized masticatory apparatus of later hominid species, particularly *A. boisei*.

#### The *A. afarensis* canine/premolar complex

The C/ $P_3$  complex of *A. afarensis* lacks the functional honing seen in extant and extinct apes (Greenfield, 1990b). Prior to the recovery of MAK-VP-1/12, the best mandibular specimen available to show the occlusal relationships of the lateral incisor, canine, and third premolar was A.L. 400-1a from Hadar. However, the lateral incisor wear in A.L. 400-1a was unusual and the A.L. 198-1 specimen lacked the incisor. The MAK-VP-1/12 Maka specimen, combined with evidence from other Hadar specimens, shows that *A. afarensis* differs from the ape condition in the arrangement and wear of these

three teeth and their maxillary counterparts, confirming previous predictions by Greenfield (1990a,b, 1992). Gorilla incisors are smaller and more vertically implanted than those of chimpanzees, whose incisors tend to wear on the lingual surface rather than in a narrow, rectangular occlusal strip. Hominids have very vertically implanted, nonprocumbent incisors that wear from the incisal edge down toward the root. In adult apes, the incisal edges and the occlusal apex of  $P_3$  lie at a level well below the canine apex. In humans, the occlusal edge of the incisors is on the same level as the C and  $P_3$  apices. The evolutionarily intermediate condition is best exemplified by the MAK-VP-1/12 specimen. Here, the incisal surface of the  $I_2$  is at the same level as the anterior edge (mesial marginal ridge) of the canine.

In *A. afarensis*, the functional incisal edge thus extends halfway across the lower canine, whose anterior apex is blunted horizontally in early wear. Posteriorly, the lower canine crown presents a sharply angled disto-inferior slope down to the level of the postcanine occlusal edge (midcrown  $P_3$ ). This canine "rise" or "step" may function to protect the third premolar and canine crowns from extreme wear in *A. afarensis* and consequently set up a steep wear gradient along the postcanine tooth row (White et al., 1981). This rise is present in younger individuals of *A. afarensis*. Most old individuals of *A. afarensis* feature first molar crown wear exhaustion (A.L. 198-1, A.L. 311-1). The  $M_1$ - $M_3$  wear gradient is extreme in the MAK-VP-1/2 specimen, a clear precursor to these older individuals. Such strong gradients are rarely seen in apes.

#### Early *Australopithecus* systematics and evolution

Among the recurrent controversies surrounding the taxon *A. afarensis* are questions regarding variation in the paratype series and pooling of the Laetoli and Hadar specimens. These have been widely discussed elsewhere, but the Maka discoveries provide a test of interpretations presenting *A. afarensis* as a single taxon (Johanson and White, 1979). The presence of both very large and very small specimens from a single horizon at Maka reinforces previous indications of extensive size variation in this taxon

(Johanson and White, 1979). The close metric and morphological matches between the MAK-VP-1/12 specimen and the L.H.-4 holotype of *A. afarensis* (Fig. 13) show that this taxon was geographically widespread.

Within the context of the detailed and dominant mandibular and dental morphological similarities between the Maka specimens and the pre-existing *A. afarensis* hypodigm, particularly noteworthy is the occurrence of a distinct root system in the MAK-VP-1/12 mandibular  $P_3$ . Although two-rooted  $P_3$ s have been previously known and described for *A. afarensis* (White, 1977; Ward et al., 1982), it is only with the unambiguous observation available for MAK-VP-1/12 that a partially molarized root form is recognized to be part of the normal species range of variation. Structurally, this root pattern may be associated with a relatively developed mesiolingual corner of the  $P_3$  crown, albeit within the normal *A. afarensis* ranges of crown variation, which differ significantly from the "molarized," "robust" *Australopithecus* condition.

Known *A. afarensis* mandibular  $P_3$  root polymorphism encompasses a wide range of structures. Some  $P_3$ s exhibit the primitive ape pattern, consisting of a mesiobuccally placed relatively columnar root and a more plate-like distal one (e.g., L.H.-4, A.L. 266-1). Within this category, the L.H.-24  $P_3$  possesses a distal root that is fully divided into buccal and lingual portions, thus effectively having three roots. Such a root pattern has recently featured prominently in the "diagnosis" of "*Australopithecus bahrelghazali*" from Chad. Other *A. afarensis* specimens exhibit the structurally simplified Tome's root condition (e.g., L.H.-14, A.L. 145-35), whereas MAK-VP-1/12 shows the partially molarized root system, a condition also approximated by some Hadar specimens (cf. A.L. 333w-60). It is not surprising that a partially molarized  $P_3$  root system is part of normal variation in *A. afarensis*, a taxon likely to be characterized by an enhanced masticatory apparatus relative to the ancestral hominid condition as discussed above. We conclude that premolar root form is highly polymorphic in *A. afarensis*, and that species-level diagnosis of early hominids should take such patterns of within-species variation more fully into ac-

count (contra Wood, 1991, and Brunet et al., 1996).

What do the Maka discoveries have to contribute to an understanding of the evolutionary relationships of the various early hominid species now recognized? The recognition of *A. anamensis* has shed new light on the early evolution of *Australopithecus*. Relative to the older *Ardipithecus ramidus*, *A. anamensis* shares with all later *Australopithecus* the derived character complex of thick molar enamel and an enlarged postcanine dentition. The most persuasive character used to distinguish *A. anamensis* from *A. afarensis* was the strong postero-inferior inclination of the symphyseal region in the former species (Leakey et al., 1995). The Laetoli holotype of the latter species has a posteriorly angled anterior corpus region relative to many Hadar mandibles, and now the Maka counterparts. It may be tempting to argue for a gradual increase in symphyseal steepness by seriating known mandibles as follows: the KNM-KP-29281 mandible (ca. 4.15 myr), the L.H.-4 mandible (ca. 3.5 myr), and the new Maka mandible (3.4 myr). The small sample sizes should, however, give us pause, particularly when combined with observations of modern chimpanzees. Here, the amount of variation between L.H.-4 and MAK-VP-1/12 or A.L. 400-1a (Fig. 10) can be matched in small ( $n = 10$ , Cleveland Museum of Natural History) samples of modern chimpanzees. It is true that the hominid symphysis became more vertical through time, but the rate at which this happened is still in the realm of conjecture, given the available samples.

We suggest that an appropriate sample with which to test proposals of evolutionary stasis in *A. afarensis* (Johanson and White, 1979; White et al., 1993) will be the enlarged Hadar collection of teeth and mandibles. These specimens, spanning the 400,000 years immediately postdating the Maka sands, will provide a more robust test of hypotheses concerning evolutionary mode and tempo than comparison of isolated frontal bones (Kimbel et al., 1994).

#### ACKNOWLEDGMENTS

Thanks go to the Ethiopian Centre for Research and Conservation of Cultural Heritage, the Ethiopian Ministry of Information

and Culture, and the National Museum of Ethiopia for permission and support; to Dr. Tekelab Mekbib for radiographic assistance; to R. Kono-Takeuchi for preparing Figure 14; to the Afar people of Gewane, Aramis, and Sagantole for field support; to Ato Alemu Ademassu for laboratory assistance; to J.D. Clark, Y. Beyene, and G. WoldeGabriel for leadership of the Middle Awash project; and to the following field workers for assistance in the 1990 work at Maka: J. DeHeinzelin, Y. Haile-Selassie, B. Latimer, K. Schick, S. Yirga, A. Negash, Z. Assefa, G. Hundie, W.K. Hart, and E. Vrba. We thank C.O. Lovejoy, D. DeGusta, H. Gilbert, three devoted reviewers, and E. Szathmáry for helpful comments on the manuscripts.

#### LITERATURE CITED

- Asfaw B. 1987. The Belohdelie frontal: new evidence of early hominid cranial morphology from the Afar of Ethiopia. *J Hum Evol* 16:611–624.
- Asfaw B. 1988. Pliocene cranial remains from Ethiopia: new perspectives on the evolution of the early hominid frontal bone. Ph.D. dissertation, University of California at Berkeley.
- Beynon AD, Dean MC. 1988. Distinct dental development patterns in early fossil hominids. *Nature* 335: 509–514.
- Boaz NT. 1988. Status of *Australopithecus afarensis*. *Yrbk Phys Anthropol* 31:85–113.
- Bromage T, Dean MC. 1985. Re-evaluation of the age at death of immature fossil hominids. *Nature* 317:525–527.
- Brunet M, Beauvilain A, Coppens Y, Heintz E, Moutaye AHE, Pilbeam D. 1996. *Australopithecus bahrelghazali*, une nouvelle espèce d'hominidé ancien de la région de Koro Toro (Tchad). *C R Acad Sci [IIa]* 322:907–913.
- Clark JD, Asfaw B, Assefa G, Harris JWK, Kurashina H, Walter RC, White TD, Williams MAJ. 1984. Paleoanthropological discoveries in the Middle Awash Valley, Ethiopia. *Nature* 307:423–428.
- Day MH, Leakey REF. 1973. New evidence of the genus *Homo* from East Rudolf, Kenya I. *Am J Phys Anthropol* 39:341–354.
- Day MH, Leakey REF, Walker AC, Wood BA. 1976. New hominids from East Turkana, Kenya. *Am J Phys Anthropol* 45:369–436.
- Dirks W. 1998. Histological reconstruction of dental development and age at death in a juvenile gibbon (*Hylobates lar*). *J Hum Evol* 35:411–426.
- Goodman AH, Armelagos GJ. 1985. Factors affecting the distribution of enamel hypoplasias within the human permanent dentition. *Am J Phys Anthropol* 68:479–493.
- Greenfield LO. 1990a. Canine reduction in early man: a critique of three mechanical models. *Hum Evol* 5:213–226.
- Greenfield LO. 1990b. Canine “honing” in *Australopithecus afarensis*. *Am J Phys Anthropol* 82:135–143.
- Greenfield LO. 1992. Origin of the human canine: a new solution to an old enigma. *Yrbk Phys Anthropol* 35:153–185.
- Johanson DC, White TD. 1979. A systematic assessment of early African hominids. *Science* 202:321–330.

- Johanson DC, White TD, Coppens Y. 1978. A new species of the genus *Australopithecus* (Primates: Hominidae) from the Pliocene of Eastern Africa. *Kirtlandia* 28: 1–14.
- Johanson DC, Taieb M, Coppens Y. 1982a. Pliocene hominids from the Hadar Formation, Ethiopia (1973–1977): stratigraphic, chronologic, and paleoenvironmental contexts, with notes on hominid morphology and systematics. *Am J Phys Anthropol* 57:373–402.
- Johanson DC, White TD, Coppens Y. 1982b. Dental remains from the Hadar Formation, Ethiopia: 1974–1977 collections. *Am J Phys Anthropol* 57:545–603.
- Kay R, Grine FE. 1988. Tooth morphology, wear and diet in *Australopithecus* and *Paranthropus* from southern Africa. In: Grine F, editor. *Evolutionary history of the "robust" australopithecines*. New York: Aldine de Gruyter. p 427–447.
- Kimbel WH, White TD, Johanson DC. 1984. Cranial morphology of *Australopithecus afarensis*: a comparative study based on a composite reconstruction of the adult skull. *Am J Phys Anthropol* 64:337–388.
- Kimbel WH, Johanson DC, Rak Y. 1994. The first skull and other new discoveries of *Australopithecus afarensis* at Hadar, Ethiopia. *Nature* 368:449–451.
- Leakey MG, Feibel CS, McDougall I, Walker AC. 1995. New four-million-year-old hominid species from Kanapoi and Allia Bay, Kenya. *Nature* 376:565–571.
- Leakey RE, Walker AC. 1985. Further hominids from the Plio-Pleistocene of Koobi Fora, Kenya. *Am J Phys Anthropol* 67:135–163.
- Leakey RE, Wood BA. 1973. New evidence of the genus *Homo* from East Rudolf, Kenya II. *Am J Phys Anthropol* 39:355–368.
- Leakey RE, Mungai JM, Walker AC. 1971. New australopithecines from East Rudolf, Kenya. *Am J Phys Anthropol* 67:135–163.
- Lovejoy CO. 1981. The origin of man. *Science* 211:341–350.
- Puech P, Albertini H. 1983. Usure des dents chez *Australopithecus afarensis*: examen au microscope du complexe canine supérieure/première inférieure. *C R Acad Sci* 296:1817–1822.
- Puech P, Albertini H. 1984. Dental microwear and mechanisms in early hominids from Laetoli and Hadar. *Am J Phys Anthropol* 65:87–91.
- Puech P, Cianfarani F, Albertini H. 1983. Tooth microwear and dietary patterns in early hominids from Laetoli, Hadar, and Olduvai. *J Hum Evol* 12:721–729.
- Puech P, Cianfarani F, Albertini H. 1986. Dental microwear features as an indicator of plant food in early hominids: a preliminary study of enamel. *Hum Evol* 1:507–515.
- Reid DJ, Schwartz GT, Dean C, Chandrasekera MS. 1998a. A histological reconstruction of dental development in the common chimpanzee, *Pan troglodytes*. *J Hum Evol* 35:427–448.
- Reid DJ, Beynon AD, Ramirez-Rozzi FV. 1998b. Histological reconstruction of dental development in four individuals from a medieval site in Picardie, France. *J Hum Evol* 35:463–478.
- Renne PR, WoldeGabriel G, Hart WK, Heiken G, White TD. 1999. Chronostratigraphy of the Miocene-Pliocene Sagantole Formation, Middle Awash Valley, Afar Rift, Ethiopia. *Geol Soc Am Bull.* 111:869–885.
- Ryan AC, Johanson DC. 1989. Anterior dental microwear in *Australopithecus afarensis*—comparisons with human and nonhuman primates. *J Hum Evol* 18:235–268.
- Simpson SW, Kunos CA. 1998. A radiographic study of the development of the human mandibular dentition. *J Hum Evol* 35:479–505.
- Simpson SW, Lovejoy CO, Meindl RS. 1990. Hominoid dental maturation. *J Hum Evol* 19:285–297.
- Simpson SW, Lovejoy CO, Meindl RS. 1992. Further evidence on relative dental maturation and somatic developmental rate in hominoids. *Am J Phys Anthropol* 87:29–38.
- Suwa G. 1990. A comparative analysis of hominid dental remains from the Shungura and Usno Formations, Omo Valley, Ethiopia. Ph.D. thesis, University of California at Berkeley. 522 p.
- Suwa G, Wood BA, White TD. 1994. Further analysis of mandibular molar crown and cusp areas in Pliocene and early Pleistocene hominids. *Am J Phys Anthropol* 93:401–426.
- Suwa G, White TD, Howell FC. 1996. Mandibular postcanine dentition from the Shungura Formation, Ethiopia—crown morphology, taxonomic allocations, and Plio-Pleistocene hominid evolution. *Am J Phys Anthropol* 101:247–282.
- Walter RC, Aronson JL. 1993. Age and source of the Sidi Hakoma Tuff, Hadar Formation, Ethiopia. *J Hum Evol* 25:229–240.
- Ward SC, Johanson DC, Coppens Y. 1982. Subocclusal morphology and alveolar process relationships of hominid gnathic elements from the Hadar Formation: 1974–1977 collections. *Am J Phys Anthropol* 57:605–630.
- White TD. 1977. New fossil hominids from Laetoli, Tanzania. *Am J Phys Anthropol* 46:197–230.
- White TD. 1980. Additional fossil hominids from Laetoli, Tanzania. *Am J Phys Anthropol* 53:487–504.
- White TD. 1984. Pliocene hominids from the Middle Awash, Ethiopia. *Courier Forschungsinstitut Senckenberg* 69:57–68.
- White TD. 1985. The hominids of Hadar and Laetoli: an element-by-element comparison of the dental samples. In: Delson E, editor. *Ancestors: the hard evidence*. New York: Alan R. Liss. p 139–152.
- White TD, Johanson DC. 1982. Pliocene hominid mandibles from the Hadar Formation, Ethiopia: 1974–1977 collections. *Am J Phys Anthropol* 57:501–544.
- White TD, Johanson DC, Kimbel W. 1981. *Australopithecus africanus*: its phyletic position reconsidered. *S Afr J Sci* 77:445–470.
- White TD, Suwa G, Hart WK, Walter RC, WoldeGabriel G, de Heinzelin J, Clark JD, Asfaw B, Vrba E. 1993. New discoveries of *Australopithecus* at Maka, Ethiopia. *Nature* 366:261–265.
- White TD, Suwa G, Asfaw B. 1994. *Australopithecus ramidus*, a new species of early hominid from Aramis, Ethiopia. *Nature* 371:306–312.
- White TD, Suwa G, Asfaw B. 1995. Corrigendum: *Australopithecus ramidus*, a new species of early hominid from Aramis, Ethiopia. *Nature* 375:88.
- WoldeGabriel G, White TD, Suwa G, Renne P, de Heinzelin J, Hart WK, Heiken G. 1994. Ecological and temporal placement of early Pliocene hominids at Aramis, Ethiopia. *Nature* 371:330–333.
- WoldeGabriel G, Renne P, White TD, Suwa G, deHeinzelin J, Hart WK, Heiken G. 1995. Age of early hominids. *Nature* 376:559.
- Wood BA. 1991. Koobi Fora research project. Volume 4. Hominid cranial remains. Oxford: Clarendon Press. 466 p.
- Wood BA, Abbott S, Uytterschaut HT. 1988. Analysis of the dental morphology of Plio-Pleistocene hominids. IV. Mandibular postcanine root morphology. *J Anat* 156:107–139.